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garden. When his cage was hung under a tree by the side-walk, the pedestrians would stop and wonder what bird that could be with so strange a plumage and so novel a song. When free in the garden Rob would have a good time of it, occasionally finding a dainty insect. But the dear fellow was getting old. Nine years is rather high for *Turdus migratorious*, and his appetite was becoming a little unnatural. He found a piece of twine, and by persevering succeeded in swallowing it. That was the worst string ever Rob got on. That western investment was the death of him.

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ON THE MORPHOLOGY OF THE SEMICIRCULAR CANALS.[1]

BY FRANCIS DERCUM, M.D., PH.D.

IN biology we meet, at every step, new and interesting questions. How this or that structure arose, what this or that fact means, are the problems which continually present themselves. The data are few and scattered, yet the attempt to arrange them in some logical manner is at least justifiable, and though our success may be doubtful, we at least take a step in the right direction.

Such an attempt let us make in regard to the semicircular canals. Under the idea that these structures, like all others, were formed for a special purpose—were designedly made to meet certain ends—a great variety of functions have been assigned to them. Viewed in the light, however, that every organ is the resultant of certain definite and interacting forces, the mere question of actual or present use becomes a secondary one. Let us see what the various facts I have collected seem to point out.

Before we attempt to understand such a complex organ as the ear, it would be well to look over the field of zoölogy to see whether we cannot find other and simpler organs of sense, which may perhaps give us the right clue. Such organs I believe to be the so-called mucous canals or lateral lines of fishes and amphibians. These structures, I need hardly say, have been ably demonstrated by Leydig, F. E. Schulze and others to be sensory. They consist essentially of small areas of nerve-epithelium arranged in linear series along the sides of the head and body, having hair-cells continuous with nerves and being in every way comparable to the maculæ acusticæ of the ampullæ and vestibule. They have received as yet no specific name. Leydig simply uses the expression "nerve-buttons" (nervenknopf), and F. E. Schulze "nerve-hills" (nervenhuegel). In the adult forms of almost all fishes, these structures are inclosed in a continuous canal formed in the epithelium. To this fact we will return again.

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[1] Read before the Alumni Association of the Auxiliary Department of the University of Pennsylvania, March 28, 1879.

The function of these organs appears to be to appreciate mass movements of the water, and more particularly vibrations which have longer periods than those appreciated by the ear.[1]

Besides the similarity in the structure of the maculæ of the lateral lines and the maculæ acusticæ, the following facts indicate a close relation between the two sets of organs. In the first place, in accordance with the general law of the development of sensory structures,[2] both the ear and the mucous canals are developed from the epithelial layer of the embryo, namely, the epiblast. Secondly, the side organs of the head are supplied by the fifth pair of nerves, while those on the body are supplied by the lateral nerves, which in turn are made up to a greater or less extent of the fifth. Now, a fact, the significance of which can never be over-estimated, is, that in the skate the auditory nerve is a primary branch of the fifth.[3]

Again, the organ of hearing is surrounded by bone really belonging to the ectoskeleton, but usually becoming incorporated with the bones of the cranium. In the same manner the side organs of the head are surrounded by bones belonging to the ectoskeleton, and likewise becoming more or less incorporated with bones of the skull and face. The supratemporals, suborbitals and lachrymals are examples of these. Even in the side organs of the body the same tendency to the persistence of bone is manifested by the occasional presence of bone corpuscles and even of cartilaginous or osseous grooves or canals. Now, while I recognize in this comparison only a very general fact, I still think that the parallelism between the bony support of the ear and the bony supports of the side organs is far greater than between the petrosal and the sclerotal.

Let us now turn to the development of the mucous canals, and see how much of general application can be gleaned from the facts. In teleost fishes the side organs first exist as mere cellular elevations[1] projecting into the water and having the percipient structures, the hairs, protected (generally, not always) by means of a delicate hyaline cylinder open at its distal end. In most cases this stage is transitory. Above and below the elevations, the epithelium of the surrounding skin becomes raised, forming a groove which is finally converted into a canal. Thus these elevations or maculæ of the side organs become enclosed by a process somewhat analogous to the involution of the ear.

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[1] See Archiv f. Mikroskop. Anat., VI. F. E. Schulze, Ueber die Sinnesorgane der Seitenlinie bei Fischen u. Amphibien.

[2] See Am. Naturalist, Sep. No., 1878. The Sensory Organs, by the writer. Also Cosmos, 1878, Oct. and Nov.. Die Enstehung des Sinneswerkzeugs, by Professor Haeckel.

[3] Owen, Comp. Anat. of Vertebrates.

In Elasmobranch fishes, however, another method is pursued. The lateral line appears already in the embryo as a fully formed canal, and, instead of being produced by an inflexion of the epiblast, is formed directly by being hollowed out in the substance of the same.[2] This departure from the general method of the development of sensory structures is an illustration of an important fact dwelt on by Herbert Spencer, namely, that the processes pursued in the development of the embryo are by no means the exact repetition of those which occurred in the evolution of the race. In many respects the processes of embryology are shortened. The integral parts or molecules of many structures tend to assume directly the relations which they occupy in the adult form, without passing through those intermediate stages which were successively traversed by the ancestors of the races.

This marked difference between the development of the lateral lines of Elasmobranchs and Teleosts is in harmony with several other interesting facts. We would naturally suppose that an organism in which a comparatively complex structure is produced by the direct method, is relatively both older and higher than one in which the same organ is produced by the indirect method. In the present instance this is the case. The Elasmobranchs constitute an order of fishes of vast antiquity, making their appearance already in the Upper Silurian, and being, therefore, among the oldest fishes known. Again, they constitute a very high order being perhaps, with the exception of the Dipnoi, the highest. They are even related in some respects to amphibians. The Teleosts, on the other hand, are ordinarily regarded as the representatives of the piscine type ; that is, as presenting preëminently those characters which constitute a fish. Secondly, the Teleosts are an order which is comparatively very young, not making its appearance until the Cretaceous period. Observe how these facts accord with the development of the lateral line. In Teleosts the involution of the maculæ or nervehills of the lateral system and the consequent formation of a canal, does not take place for days and even weeks after the young fish has left the egg. In one instance, *Gobius minutus*,[1] it does not take place at all. In Elasmobranchs, however, as stated, the canal is already formed in the embryo.

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[1] The nervehills of F. E. Schulze.

[2] See Balfour's Monograph of the Development of Elasmobranch Fishes, 1877.

Surely such a harmony of facts must be of significance, and they must open our eyes very widely with regard to the relation between embryological and race development, or, to use the words of Prof. Haeckel, between ontogeny and phylogeny. Doubtless in the primitive Elasmobranchs, or in their ancestors, the development of the mucous canals was similar to that of the Teleosts of the present day, but, in the countless repetitions during countless ages, the process was shortened and made, as we find it, immediate and direct.

Now, what bearing have such facts as these on the correct understanding of the embryology of the ear? Let us see.

Can we suppose that a structure as old as must be the organ of hearing, is still formed in the embryo by repeating the various stages once traversed by our remote ancestors? Would it not be more philosophical to expect that this organ is now produced by a process more or less direct? To this latter view I think we must, by necessity, incline.

The embryology of the ear may be briefly stated, as follows: It first makes its appearance as a depression of the epiblast in the neighborhood of the hind-brain. This depression gradually deepens until, by the coalescence of its edges, it is converted into a closed cavity. This cavity then rapidly enlarges and certain dilations or protrusions of its surface into the surrounding mesoblast take place. These protrusions are severally converted into the semicircular canals and cochlea. In the case of the semicircular canals each dilatation becomes flattened, and, by the meeting and coalescence of its opposite walls in the middle, its peripheral portion is converted into a tube, both ends of which remain permanently in communication with the primitive vesicle. The cochlear protrusion undergoes no such transformation but is simply prolonged, forming the true membranous cochlea or scala media of mammals; but with this we have at present nothing to do.

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[1] See F. E. Schulze, loc. cit.

Evidently the first stage of the development of the ear, the process of inflexion, belongs to the indirect method, but the fact that this process is still so pronounced, and the fact that the otic vesicle when once shut off from the epiblast rapidly enlarges, so that the area of the enclosed surface is relatively very great, would indicate to my mind that in our remote ancestors, this process of inflexion was very marked—that it was extensive, involving a a comparatively large area, and bringing about great modifications of structure. The tendency in the constant repetition of this process would be to diminish its relative importance, *i. e.*, to make it constantly less and less pronounced. Probably, therefore, the amount of surface actually inflected in the embryo is small compared with the area inflected in the process of ancestral development. To this we will presently return.

The special parts of the labyrinth appear to be formed by a direct method. This would, of course, as we have seen reason to believe, not exclude the possibility of an indirect method having obtained in our remote progenitors.

Having now compared the various methods pursued in the development of the mucous canals and the ear, let us recall a fact which has not yet been brought into sufficient prominence, namely, that the structure of the mucous canals and that of the semicircular canals is very similar. In 1850 Leydig[1] already noticed this fact, for he compares a semicircular canal and its ampulla with a mucous canal and its "nervebutton." Both structures consist of connective tissue lined with epithelium, and the "nervebutton" of one corresponds to the macula acustica of the other. The analogy seems complete.

Would it now be too hazardous to suggest that two organs which are so closely related in structure, which present such significant facts, as regards nerve supply and embryological development, are related genetically? Such a supposition would evidently not be inconsistent. Let us see how it may have been brought about. In an organism provided with a general apparatus for the perception of vibrations, evidently the first thing that would take place would be a specialization of certain portions for certain classes of vibrations. This is what may have been the case with the lateral canals and the ear, each being a specialization in its own peculiar direction.[1] The fact that the involution of the side organs in Teleosts does not take place until the organism is already far advanced towards the completion of its development, and the fact that the mucous canal in the embryo of Elasmobranchs does not appear until the epiblast has been differentiated into its two layers, both imply that the side organs had for ages existed as mere "nerve-hills," or nerve epithelium, projecting into the water, and this renders our idea not only possible but probable. In the course of the evolution of the ear the first differentiation of structure that occurred may have been as follows: Certain of these areas of nerve-epithelium or sensory maculæ, may, for functional specialization, have become enclosed in canals. (The great functional advantage of this form of involution over the closed vesicle, we shall presently see.) Now, for still greater specialization, the whole area containing the canals with perhaps one or two maculæ not yet enclosed, may have undergone a general process of involution and thus given rise to the vestibule and semicircular canals.

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[1] Mueller's Archiv.—Schleimkan. d. Knochenfische.

This view of the evolution of the ear is favored by the fact that the semicircular canals are *constant structures in all vertebrates!* Again, their number is always the same, namely, three, with but two exceptions, which may be easily explained. I refer to the Myxines which have but one, and the lampreys which have but two. Probably no naturalist who accepts the theory of evolution, looks upon the selachians or any other existing order of fishes as ancestrally related to the other vertebrates, and even the structure of the Marsipobranchs indicates that they belong to an *early differentiated* and highly aberrant type.

In studying the gradual development of the ear, palæontological evidence, unfortunately, cannot come into play. It is too fragmentary. The very first vertebrates that we find are already fishes of a high degree of development.

Let us now see to what views of the functional value of the semicircular canals, the above discussion leads. The first question that arises in our minds is, what is gained by the involution of the sensory maculæ? And secondly, why should this process have resulted in the formation of canals? Why did not each macula become enclosed in a separate cavity? Probably the benefit derived by a delicate sensory structure from the formation of a wall about it, is at first of a protective character, and the final formation of a cavity is the further attainment of the same end. This, however, would entail a greater or less modification of function. The exposed sensory macula would probably perceive vibrations clearly and distinctly. As soon, however, as enclosure in a cavity takes place, interference of the vibrations by their continued reflection from the walls of the cavity must necessarily occur. Such a condition of affairs is probably present in sensory structures like the "mucous" ampullæ of sharks and rays and the Savian vesicles. This difficulty is overcome if, instead of there being a cavity closed on all sides, the macula is situated in a tube. Then interference would either not result at all, or be greatly diminished, for the vibrations would be dispersed in one or two definite directions. The formation of such a structure may have been the first step in the evolution of the ear. Indeed, its parallel is presented to us in the lateral lines. The very same conditions obtain.

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[1] In this category it would be no more than just to include such structures as the *sensory ampullæ* of sharks and rays and the *Savian vesicles.*

The question now arises, when the area containing the structures about to form the ear became involuted, in what way was the function of the tubes converted into the semicircular canals modified? In other words, what is the function of the semicircular canals? The fact that both ends of each canal communicate with the utriculus, probably lessens their use as dispersing vibrations, but at the same time another and very important condition obtains. The utriculus, a comparatively small cavity, has the area of its enclosed surface materially diminished by the presence of five openings, three of which are comparatively large. In this way the capacity of its walls for reflecting vibrations must be considerably lessened, and interference of vibration consequently much diminished. Thus one function of the semicircular canals is probably to assist clearness of perception,[1] and in this respect their function would be intrinsically the same as that of the canals of the side organs. It has at various times been argued that the semicircular canals prevent interference of vibrations by the sound waves entering the same canal at opposite ends, and then meeting in opposite phases, thus mutually destroying each other. How this could occur I cannot imagine; there is no special contrivance at either end of a canal by which the vibrations would be retarded just half of a wave-length, and there is no reason why such an assumption should be made. On the contrary, I cannot see anything to prevent the waves from meeting in exactly the same phases. If so, the effect of the semicircular canals would be to increase the intensity of sounds.

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[1] This was the idea of Prof. Jackson, formerly of the University of Pennsylvania.

Various other uses have, at times, been assigned to the semicircular canals, such as the estimation of the direction of sound, or even the appreciation of pitch, besides which, conclusions have been drawn based on vivisection. Theories concerning pitch were held prior to the understanding of the structure of the cochlea, and may be dismissed without discussion. Those concerning the direction of sound are not borne out by fact. In the first place, as the contradictory results of investigators show, the power among animals of distinguishing the direction of sound is not well marked, and even if it were it would be no proof that this power lies in the semicircular canals. Again, it is self-evident that the direction of sound cannot be maintained while passing through the auditory meatus and tympanum, and if we are told that the semicircular canals appreciate vibrations transmitted by the skull, the conditions are singularly unfavorable, for just in those animals in which an appreciation of the direction of sound would seem the most important, *i. e.*, birds and mammals, the head is generally covered by a non-conducting material, feathers or hair.

The power of distinguishing the direction of sound seems to me rather to be connected with the degree of development of the auricle and the degree of its movability, or the power the animal has of quickly adapting the head to various positions, so that it can determine that position in which the impression is received the most strongly, and thence infer the direction of the sound.

The theories based on the vivisection of the semicircular canals, involve a method of reasoning that to me is not logical. To say that the results of a terrible mutilation of one of the most highly specialized parts of the body, namely, the head, are due to the destruction of any one organ or part contained in it, is certainly reasoning from incorrect premises—is certainly leaving out a large class of the facts. Secondly, to predicate that the function of an organ is the inverse of certain phenomena obtaining by its mutilation, is less logical still. To my mind the experiments of Flourens, Goltz and others, do not demonstrate that the results were due *only* to the mutilation of the semicircular canals, or that even if this were the case, anything could be predicated concerning their function. To use an apt illustration, let us take a watch and let us imagine that it was to us a new and strange machine, the various functions of which we wished to determine. Now, what would we think of a man who would plunge a knife through crystal, dial, mainspring and all, to find out how the thing worked. Is the proceeding in the case of an animal any less absurd? Is it more encouraging to know that the machine with which we are dealing is infinitely more complex, and of the fundamental truths of whose construction we can only gain vague and fragmentary ideas?

In order to understand a complex organ—if, indeed, the attainment of such an end be possible—I believe that we must cast about for the most widely scattered facts, and then view these in the broadest possible light. I believe, therefore, that the only way to understand an organ for the perception of sound vibrations, is also to study organs for the perception of allied vibrations, and then to compare the various principles involved in the development, structure and function of each. By the pursuance of such a method in the present instance, the conclusions which seem to be pointed out, are, first, that the chief significance of the semicircular canals is *morphological*, and secondly, that their functional importance, though considerable, is secondary. If, in the above discussion, I have merely raised this view of their nature to the degree of a probability—which is the most that circumstances allow—my object is accomplished.

Addendum.—After the reading of the above paper, Dr. A. J. Parker offered a suggestion with regard to the function of the semicircular canals which makes the parallelism between these structures even more apparent. His view, which he permitted me to append, is as follows:

He says that the maculæ acusticæ are very probably situated in just those parts of the labyrinth on which the sound waves impinge with the greatest intensity. This being the case with the maculæ of the ampullæ, the sound-waves probably enter the ampullar ends of the canals with much greater force than they enter the non-specialized ends. Consequently, when interference takes place, it occurs in or near these non-specialized ends, *i. e.*, where there are *no acoustic spots!* Dr. Parker looks upon the semicircular canals as so many conduits to carry off vibrations after they have impinged on the maculæ of the ampullæ. This would make their function exactly analogous to that of the lateral canals.

Dr. Parker's view also explains why each semicircular canal has but *one* ampulla, and why this should be situated at the *end*, instead of other parts of the tube.